THE EFFECTS OF SALINITY STRESS ON THE RATES OF AEROBIC RESPIRATION AND PHOTOSYNTHESIS IN THE HERMATYPIC CORAL *SIDERASTREA SIDEREA*

NYAWIRA A. MUTHIGA[1]* AND ALINA M. SZMANT[2]**

[1]*Department of Oceanography, Florida State University, Tallahassee, FL 32306 and [2]Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149*

ABSTRACT

Corals are reputed to have low tolerance to salinity fluctuations. Yet the scleractinian coral *Siderastrea siderea* commonly inhabits reef zones and nearshore areas that experience salinity fluctuations of 5 to 10‰. Small colonies of this species were subjected to both long-term and sudden decreases or increases in salinity. Their rates of aerobic respiration and photosynthesis, measured as changes in oxygen concentration, were followed for up to 144 hours after the sudden changes.

Normal salinities of coastal waters near Panacea, Florida, are 28 to 30‰, but *S. siderea* was able to acclimate to 42‰ when salinity was increased slowly over a 30-day period. Neither respiratory nor photosynthetic rates of *S. siderea* were affected by changes in salinity of less than 10‰ above or below the acclimation salinity. Greater changes in salinity (either up or down) caused decreases in respiratory and photosynthetic rates proportional to the magnitude of the salinity change. Decreases in chlorophyll per algal cell and in assimilation number were associated with and possibly responsible for some of the decreases in photosynthetic rates.

These results show that *S. siderea* is able to withstand sudden and prolonged, environmentally realistic changes in salinity without measurable whole-animal effects. Further studies are needed to determine whether this species is remarkable in its ability to tolerate salinity change, or whether reef corals are more tolerant to salinity change than is generally believed.

INTRODUCTION

Observations on the distribution and vigor of coral reefs have suggested a relationship between major environmental factors and the physiological well being of hermatypic corals. In general, coral reefs only flourish within narrow ranges of salinity, temperature, and turbidity (Wells, 1957; Yonge, 1963; Stoddart, 1969; Connell, 1973; Glynn, 1973). Although there have been a few experimental studies on the effects of temperature and sedimentation on the physiology of corals, the effects of salinity remain poorly studied.

Support for the generally accepted relationship between salinity and coral reef distribution is indirect rather than experimental. Freshwater runoff or heavy rain on shallow reef flats, or coincident with low spring tides, may lower local salinities and lead to physiological damage to reef organisms. Excessive rain killed shallow water biota on reefs in Tahiti (Crossland, 1928) and Jamaica (Goodbody, 1961). Runoff following such storms may especially damage reefs close to river mouths (Squires,

1962). The outflow of freshwater from a freshwater lens along atoll margins has been suggested to limit coral growth on inner reef flats, as observed on Arno atoll (Hiatt, 1957).

At the other extreme, high salinities resulting from prolonged drought have been observed to occur in the lagoons of Turneffe Atoll, Belize (Smith, 1941). Evaporation in tide pools during low tides may also cause salinities to rise to stressful levels.

It is generally agreed that most scleractinian corals can survive only small variations in salinity, with death resulting when salinity drops below 25‰ (Edmondson, 1928) or increases above 40‰ (Jokiel *et al.,* 1974). The few experimental studies of the effects of salinity on coral mortality have reported tolerances ranging from lower limits of 17.5 to 28‰ (Vaughan, 1919; Edmondson, 1928) and higher limits of 38.5 to 52.5‰ (Wells, 1957; Edmondson, 1928). Kinsman (1964), however, found reefs growing in salinities of more than 42‰ in the Persian Gulf with large heads of *Porites* spp. flourishing at 48‰. Observations of coral reef distribution will provide by inference information on the salinity tolerances of corals, however, there is a need for systematic studies on the effects of salinity on corals.

Detrimental effects of salinity on hermatypic corals can occur due to physiological stress on the coral animal or the corals' algal symbionts. The photosynthetic products of symbiotic zooxanthellae contribute to coral metabolism (Muscatine, 1967; von Holt and von Holt, 1968). If the symbiotic relationship between coral and algae is disrupted due to salinity stress, there may be a profound effect on coral metabolism. Several studies have reported the effects of temperature and light on zooxanthellae photosynthesis (Clausen and Roth, 1975; Coles and Jokiel, 1977; Jacques and Pilson, 1980; Jacques *et al.,* 1983) but similar information on the effects of salinity is lacking. Goreau (1964) observed that flood waters during Hurricane Flora lowered the salinity to less than 30‰ for more than 5 weeks resulting in mass loss of zooxanthellae by many reef flat corals.

The objective of this study was to determine the effects of changes in salinity on coral respiration and photosynthesis. The experimental organism was the hermatypic coral *Siderastrea siderea,* which has a wider geographic distribution than most west Atlantic reef corals. It has been reported as far north as North Carolina (MacIntyre and Pilkey, 1969) and is common wherever there is shallow hard substrate in the northeastern Gulf of Mexico. It is abundant on Floridian and Caribbean coral reefs, especially in shallow reef-flat and back-reef areas where salinity fluctuations are the greatest (A.M.S., unpub. obs.). In the Florida panhandle area of the Gulf of Mexico, this species occurs as small nodules 5 to 10 cm in diameter on rocky bottoms near shore. Salinities in these nearshore areas are usually 28 to 30‰ but can drop rapidly 5 to 10‰ during periods of runoff (unpub. obs.).

MATERIALS AND METHODS

Colonies of *Siderastrea siderea* 4 to 8 cm in diameter were collected from hard-bottom outcrops located 30 to 40 meters offshore of St. Teresa Beach, Florida, at a depth of 2 to 3 meters. They were maintained in a recirculating filtered seawater system in a constant temperature room. The volume of the system was approximately 400 liters of seawater. Water was changed each time a new batch of corals was collected, so that the initial salinity was identical to that at the time of collection. Lighting of approximately 100 μEin m^{-2} s^{-1}, measured with a Licor quantum sensor, was provided by banks of four 40 watt cool-white fluorescent bulbs suspended above the aquaria. Timers controlled a 12-hour light:dark cycle.

All salinity experiments were conducted at temperatures between 22 and 26°C.

During the winter months when the field temperatures were lower, the corals were brought to laboratory temperature by slowly raising the temperature a few degrees each day. Respiration and photosynthesis measurements were made daily until the laboratory temperature was reached. After one to four days at constant temperature, the salinity change was initiated. Tests with salinity changes of 30 to 25‰, 30 to 20‰ and 30 to 16‰ were done this way. The remaining tests were conducted during the summer at the temperature at which the corals were collected.

Each salinity test was begun by measuring the rates of aerobic respiration (oxygen consumption) and photosynthesis (oxygen production) for each coral at the control salinity (salinity at time of collection). Eight to ten corals and two control chambers without corals were used in each test. Measurements were made daily for two to four days before exposing some of the corals to the new salinity. Half of the corals (n = 4 or 5) were then exposed to the test salinity. A second set of incubations were begun immediately after, with the experimental group in the test salinity and the control group remaining at the environmental salinity. Thus, the first measurement of change in respiration was measured over the first hour after exposure to a new salinity, and photosynthesis over the second hour of exposure. The corals were later returned to maintenance aquaria at their respective salinities. Incubations were repeated at 24-hour intervals for up to a week.

During incubations, daytime respiration measurements were done first by covering the incubation system with several layers of black plastic sheeting to exclude light. A second incubation in the light to measure photosynthesis by the zooxanthellae was begun immediately following the dark incubation. Individual colonies were incubated in plexiglas chambers in a water bath to maintain constant temperature. Incubations lasted from 45 to 60 minutes. The dissolved oxygen concentration (DO) of the filtered seawater used to fill the chambers was measured and the seawater bubbled with air if it was less than 95% saturation. Water samples were taken from chambers at the beginning and at the end of the incubation. DO measurements were made using the Winkler method (Strickland and Parsons, 1972). Gross photosynthetic rates (hereafter referred to as photosynthetic rates) were estimated by summing oxygen production measured in the light with oxygen consumption measured in darkness.

At the end of each experiment, coral tissues were removed from the skeletons with a jet of filtered seawater from a Water-Pik (Johannes and Wiebe, 1970) and homogenized. Aliquots of the homogenates were preserved with Lugol's iodine (Throndsen, 1978) for microscopic determination of zooxanthellae density, or filtered onto glass fiber filters for chlorophyll measurements using a fluorometric technique (Strickland and Parsons, 1972). Surface areas of each coral were measured by the aluminum foil method of Marsh (1970), and were used to normalize the oxygen flux rates of the various sized colonies (McCloskey *et al.*, 1978). Oxygen flux rates are reported as the mean (n = 4 or 5) ±1 standard deviation. Statistical comparisons between means for each treatment were done using a two-tailed *t*-test.

<div align="center">RESULTS</div>

Daytime respiration

All of the respiratory rates reported below for the salinity tests were measured during normal daylight hours. Before accepting this experimental protocol, we tested to determine whether respiratory rates measured thus were similar to respiratory rates measured during normal nighttime hours. The results (Table I) show that respiratory rates of individual colonies varied by as much as a factor of two. However, for each

Daytime versus *nighttime respiratory rates of individual colonies of* Siderastrea siderea

Colony number	Daytime respiration rate (nmol O_2 cm^{-2} h^{-1})	Nighttime respiration rate (nmol O_2 cm^{-2} h^{-1})
1	411	411
2	824	828
3	573	552
4	810	755
—	—	—
Mean	655 ± 207	637 ± 256

Each rate represents a single one-hour long measurement.

colony, respiratory measurements made during the daytime were similar to those measured at night. Therefore we accepted the procedure of measuring respiration rates during daytime incubations.

Temperature acclimation

As salinity tests were conducted year-round at similar temperatures (22–26°C), corals used in experiments conducted during the winter were necessarily exposed to large temperature increases just before exposure to salinity changes.

Respiration rates (R) of corals collected at 16°C (R = 371 ± 67 nmol O_2 cm^{-2} h^{-1}; n = 10) increased significantly when water temperatures were gradually increased to 22°C over a 72 hour period (R = 532 ± 90 nmol cm^{-2} h^{-1}; $P < 0.01$) (Fig. 1). Photosynthetic rates also increased significantly ($P < 0.005$) from 890 ± 200 nmol O_2 cm^{-2} h^{-1} at 16°C to 1462 ± 229 nmol O_2 cm^{-2} h^{-1} at 22°C during the same time period. Photosynthetic rates increased more (39%) than respiratory rates (30%). The Q_{10}s calculated according to Schmidt-Nielsen (1979) were 1.82 for respiration and 2.29 for photosynthesis.

Responses to sudden changes in salinity

Eight tests were conducted: six on the effect of decreases and two on the effects of increases in salinity on respiratory and photosynthetic rates. Corals in the first three tests (30‰ to 25, 20, and 16‰) were collected at 15°C and were brought to laboratory temperatures, as described above, before beginning the salinity changes. Two tests studied the responses of corals acclimated to 42‰ when exposed to salinities of 35 and 22‰.

The mean respiratory and photosynthetic rates of control and test groups before and at the end of the exposure periods are summarized in Table II. There was a large amount of variability between individual colonies before exposure, and mean rates of the control groups often increased or decreased during the exposure period. However, the mean rates of the controls were similar to those previously reported for reef corals (Wethey and Porter, 1976; McCloskey *et al.*, 1978; Davies, 1978; Szmant-Froelich *et al.*, 1981). The post-exposure values in Table II are the mean rates measured at the end of each salinity test, and tests varied in duration of exposure. However, whenever a significant effect was seen, it generally occurred within a few hours of exposure (Fig. 2).

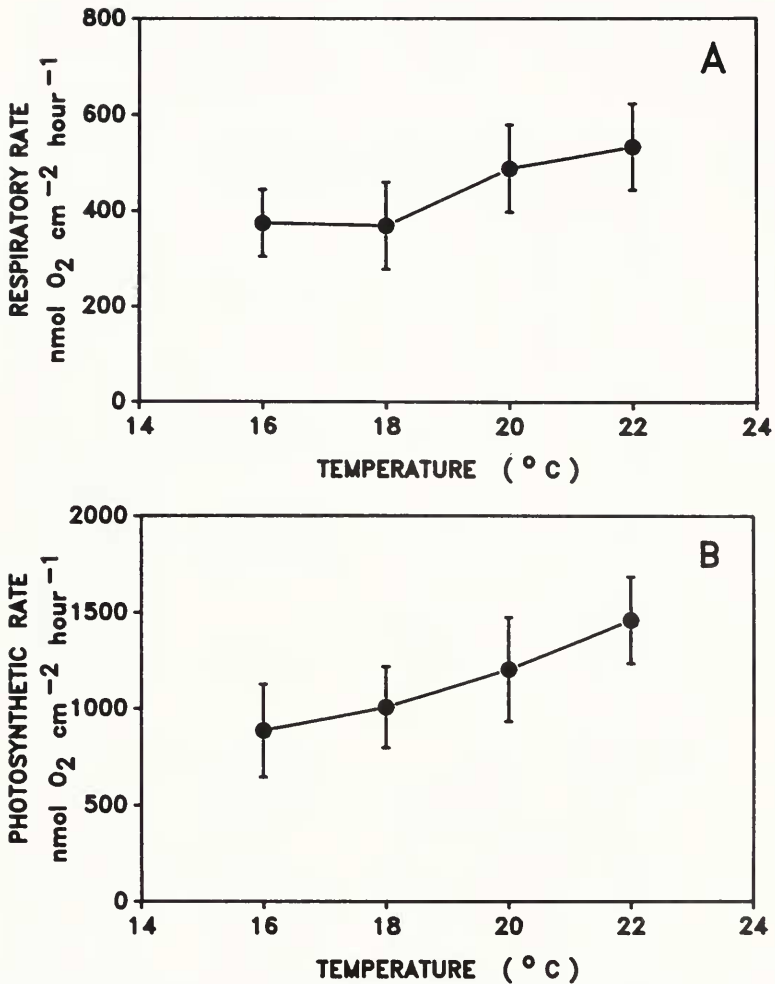Overall, the mean change in respiration of the control corals and of the corals

FIGURE 1. Mean (±1 S.D.) rates of respiration (A) and gross photosynthesis (B) of colonies of *Siderastrea siderea* exposed to 2°C increases in temperature every 24 hours. n = 10.

exposed to salinity changes of 5‰ and 7‰ was an increase of 67 ± 116 nmol O_2 cm^{-2} h^{-1} (n = 40), and this mean was not significantly different from zero ($t = 1.84$, $P > 0.05$). The mean change in photosynthesis for the same groups was an increase of 157 ± 181 nmol O_2 cm^{-2} h^{-1} (n = 40), and this mean change was significantly greater than zero ($t = 2.48$, $P < 0.02$). The gradual increase over time in photosynthesis by the control corals could be explained as a gradual adaptation by their zooxanthellae to higher light levels in the laboratory as compared to the low light levels in the muddy coastal waters where the corals were collected. These changes (increases) in respiratory and photosynthetic rates exhibited by the control corals over the one to five day experimental periods (Table II) are, in general, small and in the opposite direction to the more dramatic changes (decreases) in respiratory and photosynthetic rates exhibited by test corals exposed to the larger changes in salinity. In two cases for respiration (42 to 35‰ tests; Table II) and in three cases for photosynthesis (same two plus 42 to

TABLE II

Respiratory and photosynthetic rates of colonies of Siderastrea siderea before and after being subjected to sudden changes in salinity for up to 144 hours. Student's t-test was used to test for the significance of differences between control and experimental groups of corals at the end of the exposure period. Values are means ± 1 S.D. Values of n in ( ) can be found with the respiration results

| Salinity change | Duration of exposure (hours) | Respiration (nmol O_2 cm^{-2} h^{-1}) | | | | | Photosynthesis (nmol O_2 cm^{-2} h^{-1}) | | | | |
		Control pre-exposure	Control at end of exposure period	Experimental pre-exposure	Experimental at end of exposure period	Control vs. experimental*	Control pre-exposure	Control at end of exposure period	Experimental pre-exposure	Experimental at end of exposure period	Control vs. experimental*
Decrease in salinity											
30 to 25‰	144	452 ± 180 (15)	260 ± 59 (5)	366 ± 98 (15)	231 ± 58 (5)	n.s.	1677 ± 831	1077 ± 109	1540 ± 597	1144 ± 279	n.s.
30 to 20‰	48	280 ± 69 (20)	257 ± 51 (5)	316 ± 74 (20)	257 ± 66 (5)	n.s.	890 ± 253	650 ± 175	1001 ± 296	797 ± 215	n.s.
30 to 16‰	24	382 ± 120 (15)	429 ± 225 (5)	428 ± 64 (15)	277 ± 17 (5)	P < .025	1056 ± 298	1462 ± 229	1008 ± 245	473 ± 67	P < .025
28 to 16‰[1]	119	474 ± 52 (12)	442 ± 60 (4)	455 ± 79 (12)	286 ± 56 (5)	P < .025	1548 ± 182	1535 ± 121	1576 ± 355	709 ± 138	P < .025
42 to 35‰	94	547 ± 113 (16)	596 ± 149 (4)	419 ± 121 (16)	560 ± 46 (5)	n.s.*	1527 ± 234	1679 ± 333	1172 ± 303	1563 ± 505	n.s.*
42 to 22‰	17	626 ± 145 (12)	883 ± 43 (4)	577 ± 142 (12)	106 ± 92 (5)	P < .001	1812 ± 429	1896 ± 588	1352 ± 242	322 ± 173	P < .001*
Increase in salinity											
32 to 42‰	98	535 ± 90 (12)	536 ± 143 (4)	402 ± 70 (12)	397 ± 56 (4)	n.s.*	1421 ± 222	1807 ± 92	922 ± 112	691 ± 125	P < .001*
28 to 42‰	20	481 ± 56 (16)	498 ± 51 (4)	487 ± 83 (16)	390 ± 78 (4)	P < .025	1225 ± 188	1489 ± 156	1271 ± 320	915 ± 280	P < .025

[1] Salinity was further lowered to 12‰ over a 60 hour period before Chl a and zooxanthellae counts were made.
* Control and experimental groups were significantly different before exposure to the change in salinity; statistical comparisons were made between pre- and post-exposure rates of the experimental group.
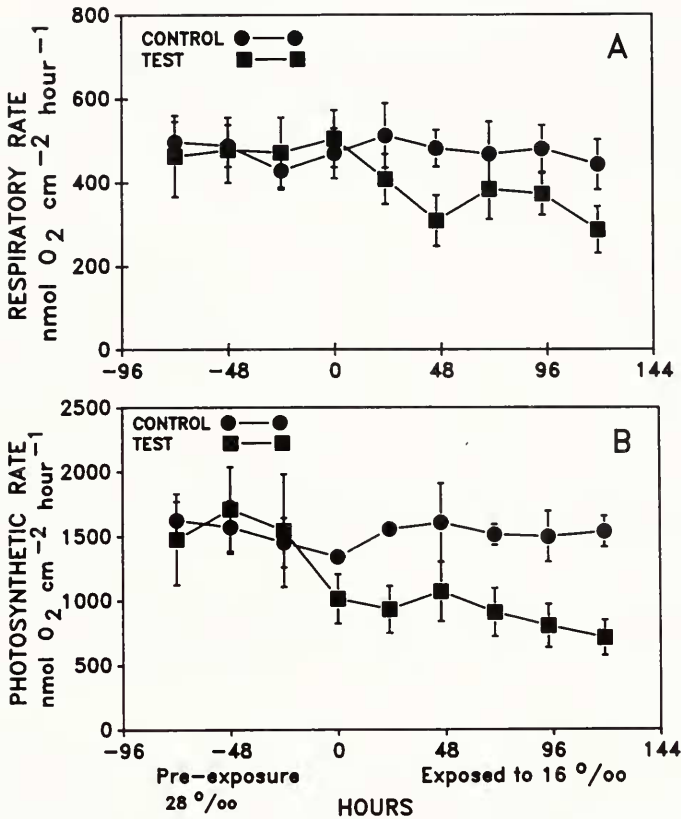
FIGURE 2. Mean ($\pm$1 S.D.) respiration (A) and photosynthesis (B) rates of *Siderastrea siderea* acclimated to 28‰ salinity and abruptly exposed to 16‰ salinity for a period of one week. n = 4.

22‰; Table II) pre-exposure rates of the control groups were significantly different from those of the experimental groups. In these cases, post-exposure rates of the experimental groups were tested against their own pre-exposure rates.

Salinity decreases of up to 10‰ (*e.g.*, 30‰–20‰) caused no significant effect on either respiratory or photosynthetic rates of test corals, but a decrease of 14‰ (from 30‰ to 16‰) caused a significant decrease in both rates (*t*-test, $P < 0.025$). Respiration decreased by 48% after 19 hours of exposure and photosynthesis decreased by 67% after 20 hours of exposure to 16‰. This particular salinity change was repeated during the summer when the ambient temperature at the collection site was the same as that in the laboratory; ambient salinity, however, was slightly lower (28‰). The corals in this later test group also showed a rapid and significant decrease in both respiration and photosynthesis when exposed to 16‰ ($P < 0.025$) (Fig. 2). Respiration decreased by 36% and photosynthesis by 33% after 44 hours of exposure, similar to the decreases observed in the first test. Further gradual lowering of salinity caused the rates of both respiration and photosynthesis to continue to decrease to 53% and 56% (respectively) of the original rates. The corals eventually died after exposure to 12‰.

Salinity increases from 32‰ to 42‰ (Δ10‰) caused no significant change in res-

Zoox[...]thellae density and chlorophyll content of the zooxanthellae of Siderastrea siderea *colonies used in the sa[...]ity tests. Measurements were made shortly after the end of each experiment. Control corals are those [...] were maintained at normal salinities throughout the test period. Test corals are those that [...] exposed to lowered salinities for the durations listed in Table II.*

Salinity change ‰	Zoox. density 10^6 cells/cm^2		Chlorophyll a μg/cm^2		Chl a/Zoox. μg/10^6 cells	
	Control	Test	Control	Test	Control	Test
30 to 25 (5)	1.49 ± 0.30	1.32 ± 0.20	9.6 ± 1.8	8.8 ± 3.0	6.6 ± 0.9	7.0 ± 2.7
30 to 20 (5)	1.46 ± 0.36	2.00 ± 0.34**	16.4 ± 4.9	14.0 ± 1.3	12.1 ± 5.5	7.1 ± 1.4
28 to 12* (4)	0.72 ± 0.11	0.53 ± 0.15	7.2 ± 1.6	3.4 ± 1.2**	10.3 ± 3.7	6.4 ± 1.8
42 to 35 (4)	0.96 ± 0.07	0.86 ± 0.07	9.1 ± 1.3	6.9 ± 1.1**	9.5 ± 2.0	8.1 ± 1.8
42 to 22 (4)	—		9.8 ± 1.7	6.7 ± 2.7	—	—
Mean	1.19 ± 0.41		10.8 ± 4.5		9.6 ± 3.9	

* This is the same test that is listed in Table II as a change in salinity from 28 to 16‰. Salinity was further reduced to 12‰ after the conclusion of the test and before the tissues were collected for the zooxanthellae and chlorophyll measurements.
** Denotes test groups that were significantly different from their controls (t-test, $P < 0.05$). Values are means ± 1 S.D. (n).

piration, but did cause a 25% decrease in photosynthesis (Table II). Corals exposed to a 14‰ increase (from 28‰ to 42‰) had significant decreases in both respiration and photosynthesis ($P < 0.025$). Photosynthesis decreased by 39% after 47 hours and respiration decreased by 22% within 43 hours.

Several colonies of *S. siderea* were gradually acclimated to 42‰ by allowing the seawater in the recirculating system to slowly evaporate over a month-long period. Respiratory and photosynthetic rates of these acclimated colonies were similar to those collected at 28 to 30‰ (Table II). When these acclimated corals were exposed to a 7‰ decrease in salinity (to 35‰) there were no measurable effects, but there were large decreases in respiration and photosynthesis when corals acclimated to 42‰ were exposed to 22‰, a change in salinity of 20‰. Respiration decreased by 82% and photosynthesis by 81% after 12 hours of exposure.

Zooxanthellae density and chlorophyll content

The control corals had variable zooxanthellae densities ranging from 0.82 to 1.49 $\times 10^6$ cells/cm^2 (Table III) in measurements made after the completion of the salinity tests. There were no significant differences between the zooxanthellae densities of control and test groups, except for the 30 to 20‰ test group which had a significantly greater zooxanthellae density than its control. The chlorophyll content of the control corals ranged from 5.8 to 17.4 μg/cm^2. In all cases, the experimental corals had lower chlorophyll contents than their control groups, but the differences were only statistically significant (t-test, $P < 0.05$) for the 28 to 12‰, and 42 to 35‰ salinity tests (Table III). In the former tests the decrease in chl a coincided with significant reductions in photosynthetic rates.

DISCUSSION

Temperature effects

Oxygen consumption is the standard method for measuring routine metabolism of an animal and is generally equated to aerobic respiration (Prosser, 1973). Within
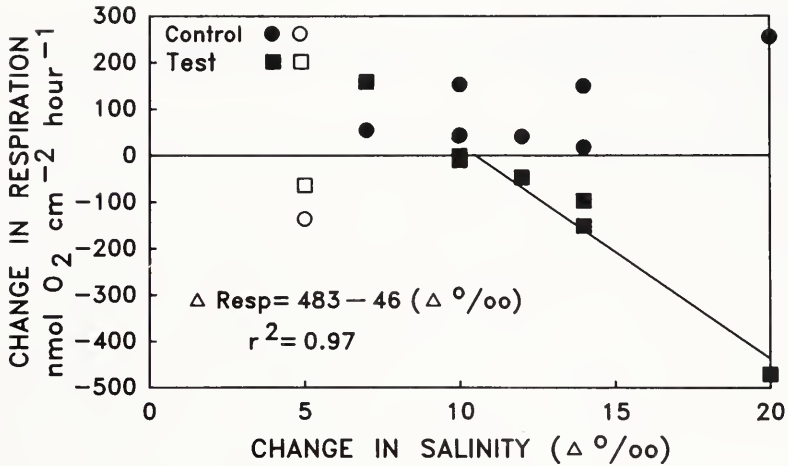
FIGURE 3. Plot of the mean change in respiration rate of colonies of *Siderastrea siderea* after 24 hours of exposure to reduced or increased salinity (Y axis) *versus* the change in salinity (X axis). Change in respiration rate was calculated for each coral as the difference between its respiration rate measured 24 hours after exposure and the mean of several measurements made over a 24 to 48 hour period before the exposure began. The changes in respiration of the control groups were plotted *versus* the changes in salinity of their respective test groups rather than opposite a zero change in salinity. The regression line was calculated using a least squares method; the 5‰ salinity change point (0) was omitted from the regression for reasons explained in the text. n = 4 or 5.

the temperature range that an organism can tolerate, the rate of oxygen consumption of heterothermic animals is often found to increase in a fairly regular manner with increasing temperature. The average Q_{10} over the temperature range of 16 to 22°C for the respiration rate of *Siderastrea siderea* was 1.82, which is similar to the Q_{10}s for respiration reported for various coelenterates (Lenhoff and Loomis, 1957; Sassman and Mangum, 1970; Mangum *et al.*, 1972). Photosynthesis is also influenced by temperature in a similar manner. The average Q_{10} for photosynthesis by the zooxanthellae of *S. siderea* was 2.29 for the same temperature range. This compares well with those found for many plants (1.0–2.7) (Salisbury and Ross, 1969).

Responses to changes in salinity

According to Vernberg and Vernberg (1972), there are several typical physiological responses to salinity stress. These include (a) an increase in respiration when subjected to salinity stress (regardless of the direction of salinity change); (b) a decrease in respiration regardless of direction of salinity change; (c) an increase in respiration if salinity is lowered but a decrease if salinity is increased; and (d) no change in respiration. In addition, there is often an initial transitory change in respiration after which a new steady state is achieved.

Siderastrea siderea shows a combination of responses (b) and (d) above, depending on the magnitude of the salinity change (Fig. 3, 4). Changes in salinity of less than 10‰ had no significant effect on respiration, nor, in many cases, on photosynthesis (response d). Thus, within the environmentally realistic salinity range for this species *S. siderea* is able to tolerate sudden and prolonged exposures to fairly large (10‰) changes in salinity. Changes in salinity greater than 10‰ and 9‰ caused significant decreases in respiration and photosynthesis, respectively, regardless of whether salin-

ity was increased or decreased (response b). There was no initial transitory burst of respiratory activity within the first hour of exposure to the altered salinity (results in Fig. 2 are representative). Rates remained lower for at least a week during the present experiments.

Figure 3 includes a least-squares linear regression of the change in respiration after 24 hours of exposure to altered salinity *versus* the change in salinity over that period. The data from the Δ5‰ test were omitted from the regression because we suspect these animals of having been incompletely adjusted to the laboratory temperature at the time the salinity change test began, and simultaneous changes in salinity and temperature may have a synergistic detrimental effect (Coles and Jokiel, 1978). All control groups (except for the Δ5‰ one) and the Δ7‰ experimental group had increases in respiration over the 24-hour experimental period. The regression shows that only salinity changes greater than 10.5‰ resulted in respiration depression. If this coral is an osmoconformer like many coelenterates (Ranklin and Davenport, 1981), its extracellular fluid osmotic pressure will fall or rise with changes in the environment. This would lead eventually to cellular swelling or shrinking, and to cell disruption. But even before such damage is done, the changes in cell size and alterations in internal geometry might disturb cell functions and possibly cause decreases in metabolic rates (Ranklin and Davenport, 1981). Alternatively, corals could contract their polyps thus reducing their contact with the adverse salinity conditions. Shumway (1978) has shown that the sea anemone *Metridium senile* contracts when exposed to lower salinity. Contraction would (a) decrease gas exchange with the exterior, and thus contribute to lower respiration rates, and (b) reduce the exposure of the zooxanthellae to light, and contribute to a lower rate of photosynthesis. However, contraction might have a similar effect on oxygen flux rates regardless of the magnitude of the change in salinity. Thus it is not a completely satisfactory explanation for the linear decrease in respiratory and photosynthetic rates that occurred as the size of the salinity change increased. No systematic observations on changes in coral behavior due to salinity change were carried out. However, casual observations revealed that *S. siderea* exposed to high or low salinities sometimes retracted into their skeletons for extended periods. Further studies should include experiments on the effectiveness of retraction as an avoidence mechanism in corals, and on the effect of retraction on the measurement of respiratory and photosynthetic rates.

The ability of this species to acclimate to abnormally high salinities (42‰) shows that the animal can acclimate to a large net salinity change when the change occurs slowly, whereas the same salinity change if experienced suddenly might be fatal. As recovery experiments were not performed, we do not know at what point the depression in respiration is still reversible upon return to normal salinities, nor whether acclimation after a sudden large salinity change will occur. In the single longer experiment where salinity effects were found early on (Table II: 28 to 16‰), respiration was still depressed after 5 days of exposure to the lower salinity.

Figure 4 shows a similar linear regression of change in photosynthesis after 24 hours of altered salinity *versus* change in salinity. The minimum salinity change that caused depression in photosynthesis was 9‰ which is slightly lower than that required to cause a depression in respiration. There were also large decreases in the chlorophyll content per algal cell in all of the test groups where it was measured, except for the 30 to 25‰ salinity change group (Table III). The decreases in photosynthesis appear to have been caused by the combined effect of small decreases in zooxanthellae density, chlorophyll content per algal cell and, in one case, by a decrease in the assimilation number (oxygen produced per amount of chlorophyll, Table IV). Polyp retraction also could have played a role as discussed above.
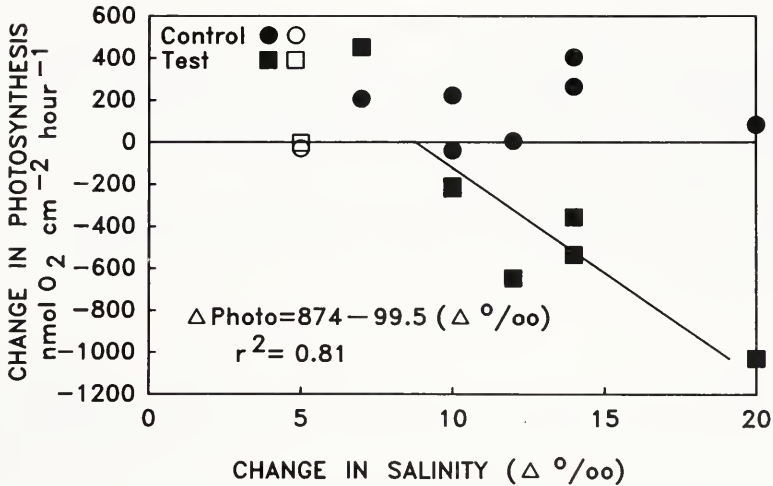
FIGURE 4. Plot of the mean change in photosynthesis rate of colonies of *Siderastrea siderea* after 24 hours of exposure to altered salinity (Y axis) *versus* the change in salinity (X axis). See legend of Figure 3 for further explanation. n = 4 or 5.

In conclusion, respiratory and photosynthetic rates of the coral *Siderastrea siderea* were not adversely affected by changes in salinity of less than 10‰, although their chlorophyll content began to decline after changes of 7‰ salinity. When exposed to salinity changes greater than 10‰ for 24 hours, respiratory and photosynthetic rates both decreased regardless of whether salinity was increased or decreased. Linear regressions showed a significant linear relationship between the degree of respiratory and photosynthetic depression and the magnitude of the salinity change. Finally, it is important to note that scleractinian corals are generally considered intolerant to salinity change, yet *S. siderea* was able to experience rather large (10‰) changes in salinity without any demonstrable effect on respiratory or photosynthetic rates. It will be interesting to determine whether this species is remarkable in this regard, and thus suited to live in reef-flat and coastal areas where salinity changes are more frequent, or whether scleractinian corals are more tolerant to salinity change than is generally believed.

TABLE IV

Photosynthetic performance by the zooxanthellae of Siderastrea siderea *exposed to changes in salinity. Duration of exposure for each test can be found in Table II*

Salinity Change ‰	nmol O_2 $(10^6$ Cells$)^{-1}$ h^{-1}		nmol O_2 $(\mu g$ chl $a)^{-1}$ h^{-1}	
	Control	Test	Control	Test
30 to 25 (5)	775 ± 135	825 ± 95	120 ± 25	138 ± 59
30 to 20 (5)	453 ± 118	393 ± 85	44 ± 19	57 ± 15
28 to 12 (4)	2173 ± 342	1350 ± 614**	222 ± 42	228 ± 133
42 to 35 (4)	1797 ± 448	1968 ± 566	188 ± 21	260 ± 121
42 to 22 (4)	—	—	192 ± 52	56 ± 35**

** Denotes test groups that were significantly different from their controls (*t*-test, $P < 0.05$). Values are means ± 1 S.D. (n).

LITERATURE CITED

CLAUSEN, D. C., AND A. A. ROTH. 1975. The effects of temperature and temperature adaptation on calcification rates in the hermatypic coral *Pocillopora damicornis. Mar. Biol.* **33**: 93–100.

COLES, D. L., AND P. L. JOKIEL. 1977. Effects of temperature on photosynthesis and respiration in hermatypic corals. *Mar. Biol.* **43**: 209–216.

COLES, D. L., AND P. L. JOKIEL. 1978. Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa. Mar. Biol.* **49**: 187–195.

CONNELL, J. H. 1973. Population ecology of reef building corals. Pp. 202–205 in *Biology and Geology of Coral Reefs,* Vol II(1), O. A. Jones and R. Endean, eds. Academic Press, New York.

CROSSLAND, C. 1928. Notes on the ecology of the reefbuilders of Tahiti. *Proc. Zool. Soc. Lond.* **Part 3:** 717–735.

DAVIES, P. S. 1980. Respiration in some Atlantic reef corals in relation to vertical distribution and growth form. *Biol. Bull.* **158**: 187–193.

EDMONDSON, C. H. 1928. The ecology of a Hawaiian coral reef. *Bull. Bernice P. Bishop Mus.* **45**: 1–64.

GLYNN, P. W. 1973. Aspects of the ecology of coral reefs in the western Atlantic region. Pp. 271–324 in *Biology and Geology Coral Reefs,* Vol II(1), O. A. Jones and R. Endean, eds. Academic Press, New York.

GOODBODY, I. 1961. Mass mortality of a marine fauna following tropical rain. *Ecology* **42**: 150–155.

GOREAU, T. F. 1964. Mass expulsion of zooxanthellae from Jamaican reef communities after Hurricane Flora. *Science* **145**: 383–386.

HIATT, R. W. 1957. Drowned ancient islands of the Pacific basin. *Am. J. Sci.* **244**: 722–791.

VON HOLT, C., AND M. VON HOLT. 1968. Transfer of photosynthetic products from zooxanthellae to coelenterate hosts. *Comp. Biochem. Physiol.* **24**: 73–81.

JACQUES, T. G., AND M. E. Q. PILSON. 1980. Experimental ecology of the temperate scleractinian coral *Astrangia danae.* I. Partition of respiration, photosynthesis and calcification between host and symbiont. *Mar. Biol.* **60**: 167–178.

JACQUES, T. G., N. MARSHALL, AND M. E. Q. PILSON. 1983. Experimental ecology of the temperate scleractinian coral *Astrangia danae.* II. Effects of temperature, light intensity and symbiosis with zooxanthellae on metabolic rate and calcification. *Mar. Biol.* **76**: 135–148.

JOHANNES, R. W., AND W. J. WIEBE. 1970. Method for determination of coral tissue biomass and composition. *Limnol. Oceanogr.* **15**: 822–824.

JOKIEL, P. L., S. L. COLES, E. B. GUITHER, G. S. KEY, S. V. SMITH, AND S. J. TOWNLEY. 1974. Final Report, E.P.A. Project No. 18050 DDN.

KINSMAN, D. J. 1964. Reef coral tolerance of high temperatures and salinities. *Nature* **202**: 1280–1282.

LENHOFF, H. M., AND W. F. LOOMIS. 1957. Environmental factors controlling respiration in hydra. *J. Exp. Zool.* **134**: 171–181.

MacINTYRE, I. G., AND O. H. PILKEY. 1969. Tropical reef corals. Tolerance of low temperatures on the North Carolina continental shelf. *Science* **166**: 374–375.

MANGUM, C. P., M. J. OAKES, AND J. M. SHICK. 1972. Rate-temperature responses in scyphozoan medusae and polyps. *Mar. Biol.* **15**: 293–303.

MARSH, J. A. 1970. Primary productivity of reef building calcareous red algae. *Ecology* **51**: 255–263.

McCLOSKEY, L. R., D. S. WETHEY, AND J. W. PORTER. 1978. Measurement and interpretation of photosynthesis and respiration in corals. Pp. 379–396 in *Coral Reefs: Research Methods,* UNESCO Monographs on Oceanographic Methodology, No. 5. UNESCO.

MUSCATINE, L. 1967. Glycerol excretion by symbiotic algae from corals and *Tridacna* and its control by the host. *Science* **156**: 516–519.

PROSSER, C. L. 1973. Oxygen: respiration and metabolism. Pp. 165–211 in *Comparative Animal Physiology,* Vol. I, C. L. Ladd, ed. W. B. Saunders Co., Philadelphia.

RANKLIN, J. C., AND J. DAVENPORT. 1981. *Animal Osmoregulation.* Halsted Press, New York. 202 pp.

SALISBURY, F. B., AND C. ROSS. 1969. *Plant Physiology.* Wadsworth Publishing Company Inc., Belmont. 747 pp.

SASSMAN, C., AND C. P. MANGUM. 1970. Patterns of temperature adaptation in North American Atlantic coastal actinians. *Mar. Biol.* **7:** 123–130.

SCHMIDT-NIELSEN, K. 1979. *Animal Physiology: Adaptation and Environment.* Cambridge Univ. Press, Cambridge. 560 pp.

SHUMWAY, S. E. 1978. Activity and respiration in the sea anemone *Metridium senile* (L) exposed to fluctuating salinities. *J. Exp. Mar. Biol. Ecol.* **33:** 85–92.

SMITH, F. G. W. 1941. Sponge disease in British Honduras and its transmission by water currents. *Ecology* **22:** 415–421.

SQUIRES, D. F. 1962. Corals at the mouth of the Rewa River, Viti Levu, Fiji. *Nature* **195:** 361–362.

STODDART, D. R. 1969. Ecology and morphology of recent coral reefs. *Biol. Rev.* **44:** 433–498.

STRICKLAND, J. D. G., AND T. R. PARSONS. 1972. A practical handbook of seawater analysis. *Bull. Fish. Res. Bd. Can.* No. **167.** 310 pp.

SZMANT-FROELICH, A., V. JOHNSON, T. HOEHN, J. BATTEY, G. J. SMITH, E. FLEISCHMANN, J. PORTER, AND D. DALLMEYER. 1981. The physiological effects of oil drilling muds on the Caribbean Coral *Montastrea annularis.* Pp. 163–168 in *Proc. Fourth International Coral Reef Symp.* Vol. 1, Univ. of the Philippines, Manilla.

THRONDSEN, J. 1978. Preservation and storage. Pp. 69–74 in *Phytoplankton Manual.* UNESCO Monographs on Oceanographic Methodology, No. 6. UNESCO.

VAUGHAN, T. W. 1919. Corals and the formation of coral reefs. *Ann. Rep. Smithsonian Instit.* **17:** 189–238.

VERNBERG, F. J., AND W. B. VERNBERG. 1972. *Environmental Physiology of Marine Animals.* Springer-Verlag, New York. 346 pp.

WELLS, J. W. 1957. Coral reefs. *Mem. Geol. Soc. Am.* **67:** 608–631.

WETHEY, D. S., AND J. W. PORTER. 1976. Habitat-related patterns of productivity of the foliaceous coral *Pavona praetorta.* Pp. 59–69 in *Coelenterate Ecology and Behavior,* G. O. Mackie, ed. Plenum Publ., New York.

YONGE, C. M. 1963. The biology of coral reefs. Pp. 209–260 in *Advances in Marine Biology,* Vol. 1, F. S. Russell, ed. Academic Press, New York.